RIFFLE BEETLES (COLEOPTERA: ELMIDAE) OF DEATH VALLEY NATIONAL MONUMENT, CALIFORNIA

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ABSTRACT — Three species of Elmidae occur in Death Valley National Monument: *Stenclinis calida* is in three springs in the Ash Meadows area; *Microcyllocpus formicoidcus* is only in Travertine Springs; and *Microcyllocpus similis* is in several springs throughout Death Valley and Ash Meadows. Only permanent springs support elmids. Considerable morphological variation occurs in the disjunct populations of *M. similis*. The evolution of elmids in Death Valley National Monument is equivalent to that of the local pupfish (*Cyprinodon* spp.).

Key words: Death Valley, Insecta, Coleoptera, Elmidae, distributions, desertification, evolution.

Death Valley National Monument (DVNM) is located mostly in southeastern California, with two small extensions into southwestern Nevada. DVNM includes Death Valley proper, its adjacent mountain ranges, and the Ash Meadows area of Nevada which surrounds Devil's Hole. Biogeographically this is a transition area between the Mojave Desert and the Basin and Range Desert. Desert conditions here are the result of the drier and warmer post-Pleistocene climate and a rain-shadow effect from the Panamint Mountains, the Sierra Nevada, and the Coast Range mountains to the west.

Water sources in DVNM are unexpectedly common. Palmer (1980) cites over 100 springs alone. Hunt (1975) has classified these springs into four types based upon volume of discharge and geomorphic origin. The Amargosa River flows (when it does!) into the southern end of Death Valley. Two permanent streams, Salt Creek and Furnace Creek, are located in the central portion of DVNM. Numerous "wells" (shallow, subsurface water sources) and "seeps" are to be found scattered throughout DVNM. These are not reliable water sources, being more or less intermittent. Wherever a water source does occur, however, it may not be very amenable to aquatic organisms because of lethal temperatures and/or salinities. Discussions of the local hydrology can be found in Hunt et al. (1966) and Soltz and Naiman (1978).

Of the aquatic organisms occurring in DVNM, only the fishes have been studied extensively. Soltz and Naiman (1978) reviewed the past work and presented an excellent synthesis, particularly so for *Cyprinodon* spp. (pupfish). For aquatic insects, studies have been primarily descriptions of new species and their type localities [e.g., Chandler (1949), Usinger (1956)]; only one study (Colburn 1980) directly addressed the ecology of any species. However, Deacon (1967, 1968) discussed insects as part of the community ecology of Saratoga Spring.

During a vacation 1 found a single specimen of a riffle beetle in Saratoga Spring at the south end of DVNM. That chance discovery led me to embark on a survey of the water sources in DVNM to determine if other elmids (riffle beetles) occurred there, and, if so, in which sources.

METHODS

Water Sources

The water sources examined were chosen primarily because of their accessibility. Those that required more than a day's travel by auto and/or foot were not examined. In all, 27 water sources were examined in Death Valley and its environs, and in Ash Meadows. Death Valley water sources include: Grapevine Spring, Scotty's Castle Spring, Mesquite Spring, Daylight Spring, Hole-in-the-Wall Spring, Midway Well, Stovepipe Wells, Salt Creek, Nevare's

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Springs, Texas Spring, Travertine Springs, Emigrant Spring, Navel Spring, Tule Spring, Badwater, Shorty's Well, Eagle Borax Spring, Warm Spring, Ibex Spring, and Saratoga Spring. Ash Meadows water sources include: Indian Spring, School Spring, Devil's Hole, Point of Rocks Spring, Jackrabbit Spring, Big Spring, and an unnamed spring.

The only permanent water sources are largevolume springs on the east side of Death Valley and in Ash Meadows, and Devil's Hole. No water flows from Devil's Hole, but here the surface of the ground intersects the hydrologic head of the groundwater so water is always present in the bottom of a large crevice. These permanent sources are all connected with the Ash Meadows Groundwater Basin.

Collections

All of the above water sources were examined for the presence of rifile beetles. Where possible, collecting was accomplished with a standard kick-net. However, many of the seeps and wells had such low discharge and/or narrow width that collection could be done only by manual removal of rocks and sticks for visual examination. Voucher specimens for all species collected were deposited in the author's collection at California State University–Sacramento.

RESULTS

Of the 27 water sources examined, 8 were found to contain populations of elmids (Table 1). Stenchnis calida Chandler was still resident in Devil's Hole, its type locality. However, during this survey two additional populations were located in nearby Indian Spring and Point of Rocks Spring. La Rivers reports unsuccessfully searching springs near Devil's Hole in an attempt to locate additional populations (Chandler 1949). It is not known whether these additional populations were missed or if they are the result of colonization or transplantation. The spring run coming from Indian Spring is very narrow and deeply incised into the desert floor, making it extremely inconspicuous.

Microcyllocpus formicoideus Shepard occurred only at Travertine Springs (Shepard 1990). Near the spring heads (a complex of several upwellings) and for many meters below, *M. formicoideus* was the only elmid to be found. Further downstream, though, it co-occurs with *M. similis* (Horn). In the lower third of the TABLE 1. The occurrence of riffle beetles (Coleoptera: Elmidae) in water sources of Death Valley National Momment.

Water source	Average temp. (C)	Elevation (m)	Species ^a
Death Valley			
1. Grapevine Spring	25-29	520	2
2. Nevare's Springs	_	300	2
3. Travertine Springs	32-36	122	2,3
4. Saratoga Spring	26 - 29	-46	2
Ash Meadows			
5. Indian Spring	24-30	705	1,2
6. Devil's Hole	**	735	1
7. Point of Rocks Spring	**	705	1.2
8. Big Spring		651	- 2

¹Γ = Stenelnus calida. 2 = Microcylloepus similis, 3 = Microcylloepus formicoideus

spring run *M. similis* completely replaces *M. formicoideus*. *Microcylloepus similis* also occurs in several other springs: Grapevine Spring, Nevare's Springs, Saratoga Spring, Indian Spring, Point of Rocks Spring, and Big Spring.

All water sources inhabited by elmids were located either on the east side of Death Valley or in Ash Meadows. With the exception of Devil's Hole, these springs all exhibit permanent flow of a relatively large volume. Most of the water sources not inhabited by elmids are low-volume seeps (e.g., Daylight Spring), subsurface sources (e.g., Shorty's Well), or pooled water (e.g., Badwater).

(Note added after author review: Richard Zack [Washington State University] has found *S. calida* in Skruggs Spring and Mexican Spring in Ash Meadows [WDS].)

DISCUSSION

The major factor linking those springs inhabited by elmids is their association with the Ash Meadows Groundwater Basin. This large watershed undoubtedly maintains the constant flow required by elmids. The only large-volume spring not inhabited by elmids, Jackrabbit Spring, was pumped dry during a local battle over water rights.

Although it may at first seem incongruous to find riffle beetles in a desert area, one must remember that the regional descritification is a rather recent event, geologically and ecologically speaking. During the several Pleistocene glacial periods, and perhaps even before, the Basin and Range Desert was far cooler and GREAT BASIN NATURALIST

wetter. The Death Valley area is thought then to have had a climate much like the present-day Lake Mono area, 240 km (150 mi) to the north (Hildreth 1976). Evidence from the distributions of fishes in the desert of California and Nevada and along the East Front of the Sierra Nevada suggests that many of the Pleistocene lakes overflowed their basins and were connected by extensive river systems (Miller 1946, Hubbs and Miller 1948, Soltz and Naiman 1978). Thus, pre-Pleistocene distributions of aquatic organisms would have been subject to changes during the Pleistocene. Ultimately, these distributions were then subjected to the influences of the warmer and drier, current interglacial period. Present distributions are, therefore, the sum of pre-Pleistocene distributions, Pleistocene dispersals, and post-Pleistocene vicariant strandings.

Small, isolated populations that were stranded in reliable water sources presented ideal situations for rapid evolution, given the small gene pools and lack of gene flow from other populations. These factors have been responsible for the quick proliferation of pupfish taxa in the Death Valley area (Soltz and Naiman 1978). This may also account for the speciation of *M. formicoidcus*, the development of subspecies in *S. calida*, and the interpopulational variation in *M. similis*.

Stenelmis calida had been previously reported from Ash Meadows in the form of its nominate subspecies. A second subspecies, S. c. moapa La Rivers, occurs southeast of DVNM along the Muddy River in southern Nevada. Each of the various populations of *M. similis* exhibits minor morphologic variations, some even in the aedeagus. I have vacillated for a long time concerning the taxonomic status of these disjunct populations. However, since the genus needs revision, and because I suspect that the variation is ecologically induced. I have chosen to be conservative and not assign separate taxonomic status to any of the populations. Perhaps some enterprising future student will examine how constant warm temperatures influence morphologic expression in riffle beetles. If so, the springs of DVNM and the Basin and Range Desert would offer an excellent natural experiment, and the numerous populations of M. similis in those springs and spring runs would be choice study material.

The elmids of DVNM represent an invertebrate analog of the already well-documented evolution of pupfish of DVNM (see Soltz and Naiman 1978). *Microcylloepus formicoideus* is similar to *Cyprinodon diabolis* in being located in only one water source and in being very distinct from and smaller than its congeners. *Stenchuis calida* is similar to *C. salinus* and *C. milleri* in that there are two taxa (subspecies) that inhabit two separate locations along a once free-flowing water course (La Rivers 1949). *Microcylloepus similis* is similar to *C. nevadensis* in being widely distributed but having isolated, somewhat morphologically distinct populations throughout DVNM and surrounding areas.

Elmids, like most aquatic insects, accomplish dispersal primarily by flying adults. As the post-Pleistocene desertification proceeded, water sources in the DVNM area became smaller, fewer, and farther apart. A point eventually had to be reached at which aerial dispersal became bazardous. Mutations reducing the ability to fly would then be favored; indeed, relatively rapid fixation of these mutations in the population would be expected. It is not surprising, then, that adults of all three elmids occurring in DVNM are either apterous (wingless) or brachypterous (with incompletely developed wings), and subsequently incapable of flying.

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